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Published in:
Journal of Comparative Physiology A

DOI:
10.1007/BF00657654

Publication date:
1979

J. comp. Physiol. 129, 199–205 (1979)

Journal of Comparative Physiology · A

Insect Pupil Mechanisms

III. On the Pigment Migration in Dragonfly Ocelli

D.G. Stavenga, G.D. Bernard*, R.L. Chappell**, and M. Wilson***

Biophysical Department, Rijksuniversiteit Groningen, Groningen, The Netherlands, and The Marine Biological Laboratory, Woods Hole, Massachusetts, USA

Accepted October 31, 1978

Summary. The light-dependent pigment migration system of dragonfly ocelli was studied by optical, non-invasive techniques. The median ocellus is comprised of two lateral halves, as can be demonstrated in the intact animal since illumination of the receptors in one half of the median ocellus only induces a movement of pigment located in that half. Measurable pigment migration can occur within a few seconds, but its speed and extent depends on light intensity. Dispersal of pigment, which occurs upon light adaptation, proceeds faster than retraction, which occurs upon dark adaptation. Action spectra for pigment movement have been determined in *Sympetrum* and *Anax*. The spectrum for *Sympetrum* has a prominent UV peak, moderate blue sensitivity, and very low green sensitivity. A similar profile is obtained in *Anax*, but only after intense orange adaptation which suppresses the green sensitivity. The results conform to the known spectral sensitivities of Libellulid and Aeschnid ocellar receptors. It is concluded that the photoreceptors drive pigment movement through an unknown mechanism. The effect of the migration of pigment is the selective reduction of radiant flux on the retina from luminous sources at high elevations relative to the animal's normal flying posture.

A. Introduction

In dark-adapted ocelli of odonates, pigment migration is induced by intensive illumination (von Hess, 1920, 1921). Although it can be easily followed in vivo under an incident light microscope no further account of the process exists except that by Lammert (1925). He was unable to confirm the discovery by von Hess of ocellar pigment migration in *Calopteryx*, *Aeschna* and *Libellula* either by direct observations or by detailed histology of both *Calopteryx* and *Aeschna*.

It seems worthwhile after more than half a century of silence on this topic to establish firmly the existence of the pigment migration system in dragonfly ocelli and to investigate whether it can be a helpful tool in the rapidly growing research on ocelli (reviews Goodman, 1970, 1975, 1979; Wilson, 1978) and on pigment migration serving a pupillary function in insect eyes (Mazokhin-Porshnyakov, 1969; Goldsmith and Bernard, 1974; Franceschini and Kirschfeld, 1976; Stavenga, 1979).

B. Methods and Materials

The experiments were performed during a simultaneous stay of the authors at the Marine Biological Laboratory, Woods Hole (Mass.), where dragonflies were caught at the local ponds. Pigment migration in ocelli of completely intact animals was observed in the libellulid *Sympetrum* and the aeschnid *Anax junius* under a dissecting microscope (Wild) fitted with an incident-light prism or studied microspectrophotometrically with an incident-light microscope (Leitz-Ortholux equipped with Opak illuminator, 16×/0.40 objective, and MPV photometer).

Action spectra for decreases in ocellar reflectance were obtained according to the constant criterion method (Rodieck, 1973, p. 261–265). The parameters for curve ○○○○○ of Fig. 4A are: adapted with a broad band short wavelength cut-off filter Schott OG530+KG3 filters, a criterion reflection decrease of 4% induced by a series of monochromatic flashes (10 nm bandwidth interference filters) of 40 s duration and ≧2 min between the flashes. The parameters for curve xxxxx of Fig. 4A are: adapted with the broad band short wavelength cut-off filter GG510+KG3 filters, 5% criterion reflection decrease and also 40 s monochromatic flashes and 2 min interval. (The former curve was shifted along the ordinate for a reasonable fit.) The parameters for Fig. 4B are: bright adaptation with orange light from a Schott OG550

* Department of Ophthalmology and Visual Science, Yale University, New Haven, CT 06510, USA
** Department of Biological Sciences, Hunter College of the City University of New York, NY, USA
*** Department of Neurobiology, Australian National University, Canberra, A.C.T., Australia

0340-7594/79/0129/0199/$01.40

(+KG3) adapting beam; the monochromatic flashes (again 10 nm bandwidth) were given during 40 s with interval 2.5 min. The criterion reflection decrease was 2.5%.

C. Results

1. The Process of Pigment Migration

Dragonfly ocelli display a bright, white reflecting tapetum when dark-adapted. In the median ocellus pigment is then concentrated along a medial ventral ridge (Fig. 1 A), and in the lateral ocelli pigment is accumulated in the posterior ventral corner. Upon intensive illumination the pigment starts to disperse from these stores, which are most probably outside the retinal photoreceptor cells (see Discussion); shown in Figures 1 and 2 of the median ocellus of a completely intact dragonfly *Anax junius*. The pigment dispersal proceeds along separate, defined paths, resulting in a reduction of the tapetal reflection (Fig. 1 C), especially in the ventral area (see also von Hess, 1920). Dark adaptation results in retraction of the pigment towards its initial state (Fig. 1 D).

A most intriguing fact is that the median ocellus is composed of two functionally distinct halves (see Discussion). Illumination of only one half of the median ocellus induces pigment dispersal in that part of the ocellus exclusively. In Fig. 1 B the pigment in the right half of the median ocellus (faced at the left hand side) was driven by illumination from the right. Fig. 2, photographed immediately before illumination-off (and before Fig. 1 B), is included here to demonstrate the position of the median ocellus between the compound eye junction and behind the protruded frons (see also Fig. 5).

Light-induced pigment migration has been observed in eyes of many animal species, both verte-

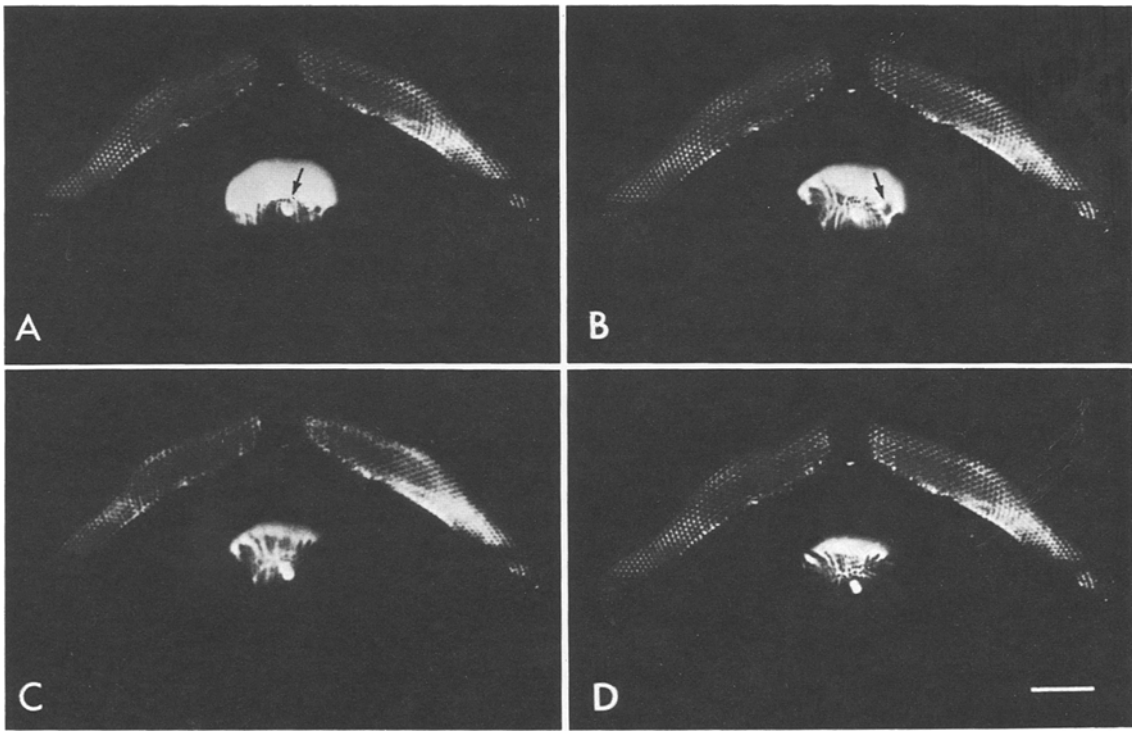

Fig. 1A–D. Pigment migration in the median ocellus of the dragonfly *Anax junius* (♀). Compound eyes at top, median ocellus at centre. Scale marker = 0.5 mm. Photographed using 15 s exposure and vertical illumination with red light (4.8 ft-cdls with Zeiss RG2 filter) which was sub-threshold to pigment migration. **A** Dark-adapted overnight. Note finger-like projections of pigment along ventral edge of ocellus having a granular appearance especially at distal ends. Bright spot on this (arrow) and other photos represents reflection of illuminator from corneal surface. **B** Light-adapted for 3 min with 300 ft-cdl. white light incident from the right. Finger-like projections of pigment extend dorsally on left side of ocellus. Dark spot on right side (arrow) is directly beneath location of corneal reflection from adapting light when it was on (see Fig. 2) and results from scattering to the retina from this spot rather than direct illumination. **C** Light-adapted for 3 min in white light from both sides. 300 ft-cdl. from right, 260 ft-cdl. from left. Finger-like projections extend dorsally on both sides of ocellus. Dark areas appear laterally on the ventral side giving the elliptical ocellus an almost triangular appearance. **D** Ocellus after 30 min dark adaptation following "C". Dorsal region is now almost clear but beaded appearance of pigment is pronounced

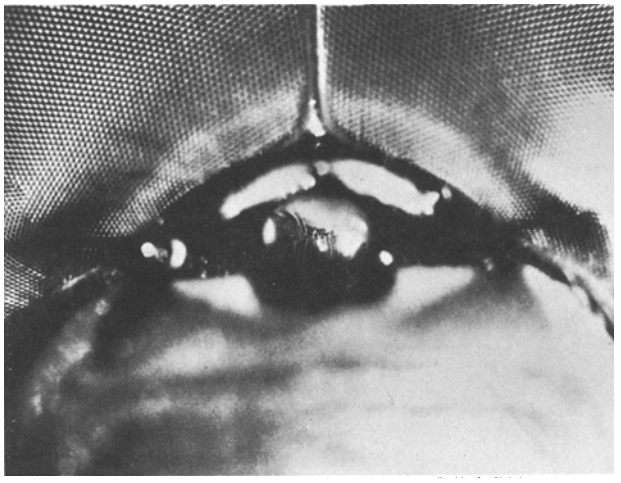

Fig. 2. Dragonfly median ocellus during light adaptation from right. Photographed using 8 s exposure with both red light (see Fig. 1 legend) and 300 ft-cdl white adapting light from right. Light-adapted 3 min. Compare with Fig. 1B which was taken immediately after turning adapting light off. Here, the junction of the dorsally located compound eyes (top) is clearly seen above the vertex which is just behind median ocellus. Antennae (out of focus) are lateral to each side of median ocellus. Finger-like projections of pigment on the left extend more dorsally and are not as blurred as in Fig. 1B where pigment is moving slowly back towards its original position after the adapting light is turned off. Magnification $\times 19$

brate and invertebrate (Mazokhin-Porshnyakov, 1969; Rodieck, 1973; Miller, 1979), and its function in the control of light on the photoreceptors has been recognized. Hence it is obvious to assume that the migrating pigment serves a pupillary function for the ocellar photoreceptors. Activation of the system does not proceed via light absorption by the migrating pigment as is evidenced by the following experiment. A light source focussed on the pigment mass in the dark-adapted state was quite ineffective in eliciting pigment movement, but rapidly induced pigment dispersal when projected more centrally onto the retina.

It therefore was hypothesized that the photoreceptors are directly involved in the pupillary mechanism. Before determining action spectra which might elucidate this point it was necessary to study the dependence of the system on light intensity. This was performed by measuring the reflectance of the ocellus via an incident illumination microscope. Figure 3 shows that pigment dispersal is intensity-dependent with respect to both speed and magnitude. Speed of retraction during dark adaptation depends on the state of the pigment. Dispersal is always much quicker (in *Sympetrum* the half time is approximately 0.5 min) than retraction (half time $\simeq 2$ min). The speed varies among species.

2. *Action Spectra*

Action spectra of the pigment migration system were obtained from both *Sympetrum* and *Anax*. Pupillary sensitivity in *Sympetrum* is pronounced in the UV, moderate in the blue, and very low for longer wavelengths (Fig. 4A). Approximately the same spectrum is obtained in *Anax* only after the ocellus has been bright adapted to a prolonged adaptation with intense orange light (Fig. 4B). In the approximately dark-adapted *Anax* ocellus a clear green peak was found. Whether these results indicate that the visual recep-

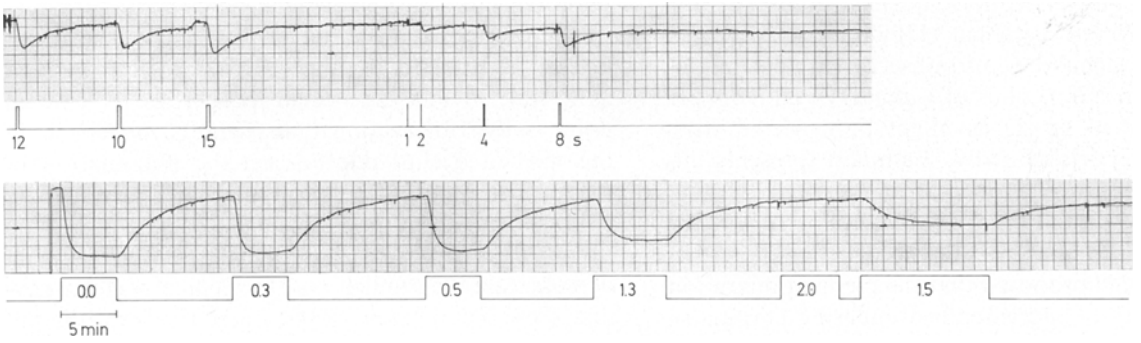

Fig. 3. Recordings from reflection changes resulting from pigment migration induced by illumination of the median ocellus of a *Sympetrum* dragonfly. The reflection of incident light of 508 nm wavelength was measured. A 508 nm interference filter was also placed in front of the photomultiplier so that the adapting beam having a broad UV-blue spectral content was cut off. Higher reflection is upward; zero is at the base of the mm-graph paper. The test beam is in the bottom trace initially shut off and delivered 1 min before the adapting beam was exposed to the ocellus. The top trace shows that the extent of pigment migration depends on the duration of (constant intensity) illumination (which is indicated in s). In the experiment of the bottom trace neutral density filters were put onto the adapting beam, and illumination was interspersed with dark times. Log_{10} density value of the applied filter used is indicated. Prolonged dark adaptation is necessary to reach the fully dark-adapted value

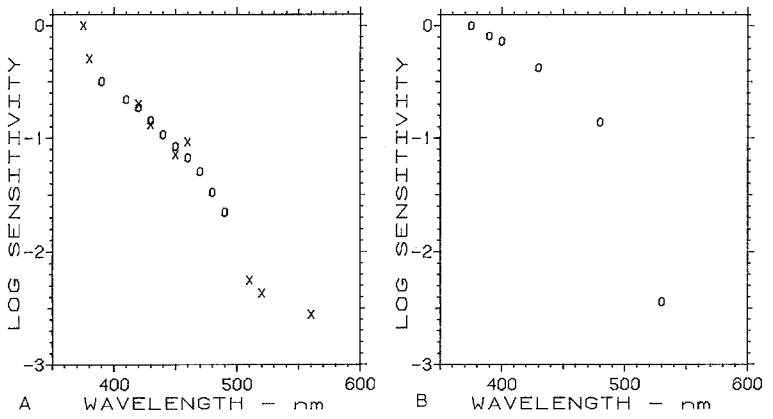

Fig. 4A and B. Action spectra of pupil mechanisms of dragonfly ocelli determined by measuring the quantum flux necessary to induce a criterion change in reflection from the ocelli.
A Data from the median ocellus of two individual *Sympetrum*.
B Spectral sensitivity of a lateral ocellus of a male *Anax* after it had been bright adapted with intense orange light (see further Methods section)

tors are involved in the pigment migration system is discussed below.

D. Discussion

1. Mechanism of Pigment Movement

Light-induced pigment migration is a generally occurring phenomenon in odonate ocelli; it has been observed in both dragonflies (Anisoptera: von Hess, 1920, 1921; this report) and damselflies (Zygoptera: von Hess, 1920, 1921).

Often Lammert (1925) is quoted also as the reference for pigment migration in dragonfly ocelli. However, in that paper a curious line of argument is presented, which is briefly as follows. Lammert (1925) first presents a long quotation of von Hess (1921) describing the severe darkening of the ocelli of *Calopteryx virgo* and *Aeschna grandis* upon illumination with day light focussed by a condensor. Then he gives an account of his inability to repeat von Hess' findings in neither *Calopteryx* nor *Aeschna*. Subsequently, Lammert (1925) reveals that Homann (no reference), with refined techniques, did observe pigment migration in the median ocellus of *Calopteryx* and *Agrion;* however, not as severe as might be expected from von Hess' reports. Finally, Lammert presents his histological results obtained from *Aeschna*. He encountered pigmented cells, chromatophores, between the lens and the retina of *Aeschna* ocelli. Therefore, Lammert (1925) proposed that the pigment migration occurs by way of individually wandering chromatophores. This explains the very granular appearance of the pigment tracts in *Aeschna* and *Anax* (Fig. 1, 2). Lammert (1925) was unable to find chromatophores in *Calopteryx* and hence could not see in which way pigment migration could occur in the ocelli of damselflies. The failure of Lammert (1925) to confirm the pigment migration by histological or optical methods can be understood to some extent from the necessity to apply quite bright light to the ocelli before pigment dispersal starts. Furthermore, the darkening of the ocellus as described by von Hess (and photographed in Fig. 1) is only apparent from particular angles of observation.

The physical forces responsible for pigment migration in eyes are not well understood. Actin-like filaments in the vertebrate pigment epithelium have been described (Murray and Dubin, 1975). In the case of *Limulus* evidence exists that microtubules are involved (Miller, 1979). The pigment migration system of dragonfly ocelli might well be a strategic preparation for the determining of the mechanisms involved, since excellent visibility of the process in intact, living animals is possible (Fig. 1); also, the process is rapid (in the locust half time is several min; see Wilson, 1975). It should be mentioned also that the dragonfly ocellus is a tractable preparation for studying pigment movement because it can be kept alive in isolation from the rest of the animal (Wilson, in preparation) and intracellular recordings can be made from its photoreceptors (see below).

Furthermore, the pupil of dragonfly ocelli is of interest to students of this organ since it can be used as a tool to analyze ocellar properties. A case in point is the observation that pigment movement in the median ocellus depends on the illumination of the proper half of the ocellus. Actually von Hess (1921) already mentioned this phenomenon in passing in *Libellula depressa*. It is interesting that one can demonstrate the duplicity of the median ocellus (Leydig, 1864; Redikorzew, 1900; Link, 1909) via the pupil mechanism in an intact animal.

This duplicity concept is supported as well by intracellular procion dye injection identification of neurons which connect a single lobe of the dragonfly median ocellus to the brain (Patterson and Chappell, 1976).

It might be worthwhile to recall here that the

3 ocelli originate from 4 rudiments, two of which subsequently merge and give rise to one ocellus according to developmental studies on hymenopterans (*Vespa*: Patten, 1887; *Formica:* Caesar, 1913; Vogt, 1946). In certain myrmicine ants, however, merging is incomplete and binary anterior ocelli remain (Wheeler, 1936; Weber, 1948).

In conclusion, the fact that the duality of the median ocellus is reflected in the movement of pigment gives an important clue for unravelling mechanisms of receptor/pigment coupling, which deserves further study.

2. *Function of Pigment Movement*

The function of the pigment migration system is most likely that of control of light incident on the retinal photoreceptor cells. In insect compound eyes pupil mechanisms are realized in different ways. Pigment migration occurs in both the screening pigment cells (e.g. in moths, mantids, neuropterans), and within the visual sense cells (e.g. in flies, hymenopterans, lepidopterans; rev. Mazokhin-Porshnyakov, 1969; Goldsmith and Bernard, 1974; Horridge, 1975; Franceschini and Kirschfeld, 1976; Stavenga, 1979). In ocelli there is also no unique type of pupil mechanism. Wilson (1975) discovered that locust ocelli possess a pupil in the form of a ring of specialized epidermal cells in which pigment moves depending on light intensity. Migration of pigment granules inside visual sense cells occurs in the ocelli of *Rhodnius* (Goodman, 1975).

That the light absorbed by the visual pigment in the photoreceptor cells mediate pigment migration is documented in a wide variety of species and in the various systems (frog: Liebman et al., 1969; squid: Hagins and Liebman, 1962; dipteran flies: Franceschini, 1972; Bernard and Stavenga, 1977, 1978; ant: Menzel, 1972; butterfly: Bernard, 1979). The comparison of pupillary action spectra to published electrophysiological data on ocellar photoreceptors, as discussed below, indicate that ocellar pigment migration is driven by ocellar photoreceptor cells.

Few spectral studies so far have been performed on insect ocelli. From measurements of the ERG a single blue-green receptor ($\lambda_{max} = 500$ nm) was found in cockroach (Goldsmith and Ruck, 1958). A high sensitivity in the UV and blue (340–450 nm), probably also originating from one spectral mechanism, was found for ocelli of the blowfly *Calliphora* (Kirschfeld and Lutz, 1977) and the fruitfly *Drosophila* (Hu et al., 1978). For the honeybee two receptor types, with maximal sensitivity in the UV (335–340 nm) and in the green (490 nm) respectively, were detected (Goldsmith and Ruck, 1958; Goldsmith, 1960). Similar results were also obtained from the ocelli of the cabbage looper moth (Eaton, 1976, $\lambda_{max} = 360$ nm and 530 nm). An unclear situation exists in the case of dragonflies. Ruck (1965) concluded from ERG measurements in *Libellula luctuosa* that bot green ($\lambda_{max} = 518$ nm) and UV receptors exist. Intracellular recordings by Chappell and DeVoe (1975) in *Anax* and *Aeschna* indicated that both spectral mechanisms contribute to responses of single cells, possibly due to either coupling of UV and green cells or because each photoreceptor cell contains two visual pigments. On the other hand, from *Libellula pulchella* Chappell and DeVoe (1975) obtained intracellular recordings pointing to a distinct UV-sensitivity much greater than that in the green while Ruck's (1965) ERG recordings indicated just the opposite. Our action spectra of the pupil can be helpful in clarifying this question since a pronounced UV-sensitivity and a very low green sensitivity was detected also in the libellulid *Sympetrum* (Fig. 4A). If one compares this spectrum to that for a UV-receptor (e.g., Bernard and Stavenga, 1978) a much elevated sensitivity in the blue emerges for the ocellus. This points to the presence of blue receptors in the *Sympetrum* ocellus. Furthermore, for *Anax* distinct UV and green spectral mechanisms were found, since the green peak could be chromatically adapted (Fig. 4B).

In this respect the absorption characteristics of the pupillary granules may reveal additional evidence. From compound eye studies it is now well recognized that the spectral absorption curve of the screening pigment is attuned to the spectral sensitivity of the photoreceptor cells (Stavenga et al., 1973, 1975; Stark, 1975; Langer, 1975; Kirschfeld and Wenk, 1976; Horridge and McLean, 1978; Laughlin and McGinness, 1978; Stavenga, 1979). The grey brown pigment of *Anax* ocelli points to a shielding function over a wide visible range. The yellow brown colour of the granules in *Sympetrum* ocelli indicates that the photoreceptors have a sensitivity range restricted to the shorter wavelengths. It thus seems that between families within the suborder of Anisopteran dragonflies distinct differences occur in ocelli at the retinal level, as has been recently established for the dorsal compound eyes of Aeschnidae and Libellulidae namely that in the former family UV, blue and green visual receptors together with black screening pigment exist, while in the latter family predominantly short wavelength receptors correlated to orange pigmentation occur (for discussion see Sherk, 1978; Laughlin and McGinnes, 1978).

From the present evidence it thus is concluded that both spectral and local illumination experiments

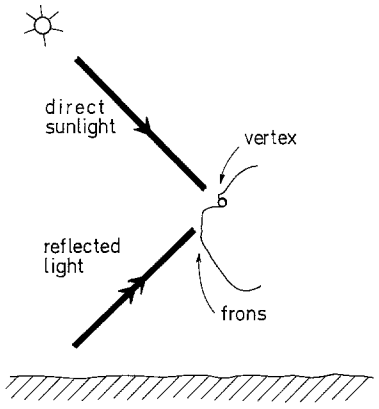

Fig. 5. Diagram demonstrating the set of visors with which a median ocellus of the dragonfly *Anax* is equipped. The dorsal vertex of the ocellus occludes the main area of the skies. The protruded frons shields the ground parts and, probably more important, the reflections from the water surface above which this dragonfly often flies. Direct sunlight impinging upon the ventral part of the ocellus is prevented from reaching the photoreceptor layer by the flexible, internal visor, the pupillary pigment

suggest that the retinal cells signal the pupil mechanism.

At the end of this discussion it may be appropriate to point to the curious fact that the pupil mechanism is only active in the ventral part of the ocellus. Figure 5 is drawn to help understand the sensible design of such a pupil. It may be recalled that commonly dragonflies are on the wing in high ambient light conditions and except for some rapid turns fly with their body axis horizontal. The field of view of the ocelli then is centered near the horizon, and direct sunlight is incident from above. This light apparently is unwanted, since, for instance above the median ocellus of *Anax*, a distinct vertex exists which functions like a visor for the ocellus. Still, when a dragonfly faces the sun direct sunlight will be projected onto the ventral areas of the ocelli. There this light is subdued by the action of the pupillary pigment. It may be interesting that in those dragonflies which spend their daily routine patrolling above ponds, like *Aeschna* and *Anax*, a huge frons has been developed. Possibly an important function of this protruded platform is to prevent reflections from the water surface to enter the ocellus so that no confusions occur for such systems as the flight stabilization system postulated for locust ocelli (see Wilson, 1978).

This work was supported by grants by the Netherlands Organization for the Advancement of Pure Research (Z.W.O.) (to DGS), by National Eye Institute U.S.P.H.S. EY01140 and EY00785 (to GDB) and EY00777 and EY00040 (to RLC).

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